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THE PHENOMENON OF SELF-STERILITY¹

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IN both animals and plants in which the two sexes have been combined in the same individual, cases have been found where self-fertilization is practically impossible. This gametic incompatibility has been called self-sterility, although the term is hardly proper as applied to normal functional gametes that may fuse with their complements in the regular manner, provided each member of a pair has been matured in a separate individual.

In plants the phenomenon has been known since the middle of the nineteenth century, in animals a corresponding discovery was made in 1896 by Castle, the species being one of the Ascidians, *Ciona intestinalis*. During the eighteen years that have passed since Castle's discovery, *Ciona* has been studied on a large scale by Morgan (1905), Adkins (Morgan, 1913), and Fuchs (1914). The botanists, however, have lagged somewhat behind; for, in spite of having been acquainted with self-sterility in plants for over half a century, and having found over thirty species where a greater or less degree of self-sterility occurs from which to select material, very few thorough investigations into the physiology of the subject have appeared.

The main facts regarding fertilization in *Ciona intestinalis* are about as follows:

1. Under uniform suitable conditions, individuals vary in degree of self-sterility, it being exceptional to find an animal that is perfectly self-sterile.
2. Self-fertility has never equaled cross-fertility, though the possibility remains that some animals may be self-

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fertilized as easily as they may be crossed with certain particular individuals.

3. The ease with which the ova of any animal "A" may be fertilized by the sperm of other individuals may vary.

Morgan (1913) concluded from his own work and that of Adkins that there were wide differences in the compatibility of ova to different sperm. Fuchs (1914) maintained that 100 per cent. of segmenting eggs can be obtained in every cross if the ova are normal and a sufficiently concentrated sperm suspension is used. It is possible that Fuchs is correct and that varying concentrations of sperm suspension were the cause of Morgan's and Adkins's results, yet the possibility of differences in this regard inherent in the individual is not to be overlooked. It will be seen later that I regard the matter as of great importance to the general subject.

4. A chemical basis for self-sterility is shown in Fuch's experiments by (a) the decrease in ease of cross-fertilization after contact of ova with sperm from the same animal, and by (b) the difference in ease of self-fertilization after various artificial changes in the chemical equilibrium of the medium surrounding the ova.

From the botanical side various studies on the physiology of self-sterility have appeared since such investigations were initiated by Hildebrand in 1866. At this time it is necessary for us to consider only those of Jost (1907), Correns (1912), and Compton (1913).

Jost was able to show that in self-sterile plants tubes formed from their own pollen were so limited in their development that fertilization did not occur, although the necessary length of pollen tube was easily developed after a cross-fertilization. He saw as the cause of these phenomena the presence of "individueller Stoffe." Pollen was indifferent to "Individualstoff" of the same plant, but was stimulated by that of other plants.

Correns (1912), working with one of the bitter cresses, *Cardamine pratensis*, obtained results to which he gave a simpler interpretation. Starting with two plants, B and

G , he crossed them reciprocally and tested 60 of the offspring by pollinating from the parents, on the parents, and *inter se*. The back crosses of $(B \times G)$ or $(G \times B)$ with B and with G apparently indicated four classes about equal in size with reference to gametic compatibility: (1) plants fertile with both B and G ; (2) plants fertile with B but not with G ; (3) plants fertile with G but not with B ; (4) plants fertile with neither B nor G .

To these facts Correns gave a Mendelian interpretation by assuming the existence of two factors each of which inhibits the growth of pollen tubes from like gametes. Representing these factors by the letters B and G , it is clear that types BB and GG could never be formed. The original plants were supposed to be of classes Bb and Gg , respectively. When crossed there resulted the four types BG , Bg , bG and bg . Plants of types BG , Bg , and bG should be self-sterile, while plants of the type bg should be self-fertile. Plants BG should be fertile with plants bg , plants Bg should be fertile with bG and bg , and plants bG should be fertile with Bg and bg . As a matter of fact Correns's results were not clearly in accord with the theory. Plants of the type bg were not self-fertile, and the other classes of matings showed many discrepancies. It is only fair to say, however, that the author recognized some of these difficulties, but believed them to be due to other inhibitors.

In a part of Compton's (1913) work, a still simpler interpretation of self-sterility is offered, at least for a particular case, that of *Reseda odorata*. Darwin's original discovery that both self-sterile and self-fertile races of this plant exist was confirmed and the following results obtained in crossing experiments. Self-sterile plants crossed either with self-sterile or with self-fertile plants gave only self-sterile offspring. Certain self-fertile plants, however, gave only self-sterile offspring when self-pollinated. Other self-fertile plants gave ratios of 3 self-fertile to 1 self-sterile offspring when self-pollinated, and ratios of 1:1 when crossed with pollen from self-sterile

plants. For these reasons he regards self-fertility as a simple Mendelian dominant to self-sterility in the case studied. I believe Compton would draw no such sharp line about self-sterility in general. In fact, he follows Jost in suggesting the presence of a diffusible substance in the tissues of the style and stigma which retards or promotes pollen tube growth after self-pollination or cross-pollination in some manner analogous to the mechanism that promotes animal immunity or susceptibility after infection.

The only alternative general hypothesis has been proposed by Morgan, and this can be discussed more advantageously after the presentation of my own work, of which only an abstract will be given at this time.

In 1909 I made a cross between a small red-flowered *Nicotiana*, *Nicotiana forgetiana* (Hort.) Sand. and the large white-flowered *Nicotiana* of the garden *Nicotiana alata* Lk. and Otto. var. *grandiflora* Comes. All of the plants of the F_1 generation appeared to be self-sterile. Tests of *Nicotiana forgetiana*² have shown these plants also to be self-sterile, but both self-fertile and self-sterile plants of the other parent have been found. From data gathered later, there seems to be no doubt that a self-sterile plant of *Nicotiana alata grandiflora* was used in the actual cross. This conclusion seems reasonable in view of the fact that of over 500 plants of the F_1 , F_2 , F_3 and F_4 generations tested, not a single self-fertile plant was found.

The plants of the F_1 generation were all vigorous and healthy, and in spite of the fact that they resulted from a species cross which Jeffrey claims always produces large amounts of abnormal pollen, a large number of examinations of pollen from different individuals showed from 90

² I thought originally that both of these species (East, 1913) were self-fertile. Seed had been obtained from a carefully bagged inflorescence of each species in 1909. Either the plant of *N. forgetiana* which gave this seed was self-fertile—something that I have never been able to find since that time—or there was an error in manipulation. At any rate, the plants resulting from this seed were all self-sterile.

to 100 per cent. of morphologically perfect pollen grains, a condition about the same as was found in the pure species. To this statement there is one exception. A single plant was found with only about 2 per cent. of good sound pollen.

Several experiments were made in which crossing and selfing was done on a large scale, using plants of the F_2 , F_3 and F_4 generations which had segregated markedly in size and were of at least 8 different shades of color. In one of these experiments 20 plants of the F_2 generation coming from 2 crosses of F_1 plants were used. It was planned to make all possible combinations of these plants, 400 in all. This task proved overburdensome, however, and in addition to the self-pollinations but 131 inter-crosses were made with the following results.

1. Each plant was absolutely self-sterile.

2. Leaving out of consideration the plant with shrunken imperfect pollen only two crosses failed. This failure of 1.5 per cent. of the crosses may have been due to improper conditions at the time of the attempts, but as a number of trials were made the possibility remains that there is a small percentage of true cross-sterility.

3. Of the 129 successful inter-crosses, 4 produced capsules with less than 50 per cent. of the ovules fertilized. The remaining crosses produced full capsules. It is barely possible that this result shows a slight variability in ease of cross-fertilization, but I am more inclined to believe that these 4 cases where a low percentage of fertilized ovules were obtained were accidental.

Other crossing experiments of the same kind have corroborated these results. Out of 120 inter-crosses, only 3 failed.

Later, something over 100 inter-crosses were made between 12 plants of an F_3 population resulting from crossing two sister F_2 plants. Six of the attempts at cross-fertilization—3 to 8 trials per plant being made—were failures. These plants as well as others tested were com-

pletely self-sterile, and apparently there was cross-sterility in about 6 per cent. of the possible combinations.

In the F_4 generation, 10 plants resulting from crossing two sisters of the F_3 generation were selected for experiment. Unfortunately, I was able to make only 58 intercrosses, 5 of which, almost 10 per cent., failed.

Back crosses have furnished another line of experiment, though they have not been carried on as systematically as were those of Correns. Nearly 85 back-crosses using plants from the progeny of four combinations which included four individuals as parents, have been made. The plants themselves all proved self-sterile, and in addition 5 of the back crosses failed.

When these experiments were begun I expected to find that the facts would accord with a simple dihybrid Mendelian formula similar to that which Correns later proposed as an interpretation of his results, yet only by considerable stretching and a vivid imagination will Correns's data fit such an hypothesis, and my own data do not fit at all. No self-fertile plants have been produced by any combination, and cross-sterility is a possibility in only from 1.5 to 10 per cent. of the combinations. Furthermore, Correns's idea of inhibitors appears unlikely from some other data I have gathered with the help of Mr. J. B. Park. Ten plants were involved in this experiment. Pairs of plants were provided to furnish series of selfed and crossed flowers. The pistils of these flowers were fixed at regular periods after pollination, stained, sectioned, and the pollen tubes examined. Fertilization not later than the fourth day marked the end point of the crossed series, the dropping of the flowers between the eighth and the eleventh day ended the selfed series. As the flowers on each plant had about the same length pistils, curves of pollen tube development for both crossing and selfing could be constructed. The pollen grains germinated perfectly on stigmas from the same plant, from 1,200 to 2,000 tubes having been counted in sections of single pistils. The difference between the development

of the tubes in the selfed and the crossed styles is wholly one of rate of growth. The tubes in the selfed pistils develop steadily at a rate of about 3 millimeters per twenty-four hours. There is even a slight acceleration of this rate as the tubes progress. If the flowers were of an everlasting nature one could hardly doubt but that the tubes would ultimately reach the ovules, though this would not necessarily mean that fertilization must occur. Since the maximum life of the flower is about 11 days, however, the tubes never traverse over one half of the distance to the ovary. On the other hand, the tubes in the crossed pistils, though starting to grow at the same rate as the others, pass down the style faster and faster, until they reach the ovary in four days or less.

From these facts it seems reasonable to conclude that the secretions in the style offer a stimulus to pollen tubes from other plants rather than an impediment to the development of tubes from the same plant.

The whole question, therefore, becomes a mathematical one, that of satisfying conditions whereby no stimulus is offered to pollen tubes from the same plant, but a positive stimulus is offered to tubes from nearly every other plant.

Morgan has given an answer to this question in a general way. If I understand his position correctly, my own conclusions are not very different from his, but are somewhat more definite. Morgan (1913) states that the results of Adkins and himself on *Ciona intestinalis* can best be understood by the following hypothesis:

The failure to self-fertilize, which is the main problem, would seem to be due to the similarity in the hereditary factors carried by the eggs and sperm; but in the sperm, at least, reduction division has taken place prior to fertilization, and therefore unless each animal was homozygous (which from the nature of the case cannot be assumed possible) the failure to fertilize can not be due to homozygosity. But both sperm and eggs have developed under the influence of the total or duplex number of hereditary factors; hence they are alike, *i. e.*, their protoplasmic substance has been under the same influences. In this sense, the case is like that of stock that has long been inbred, and has come to have nearly the same hereditary complex. If this similarity decreases

the chances of combination between sperm and eggs we can interpret the results.

I make this quotation to show Morgan's viewpoint. It is for him to say whether the following conclusions are extensions of his own or not.

The tolerably constant rate of growth of pollen tubes in the pistils of selfed flowers, compared with the great acceleration of growth of the tubes from the pollen of other plants as they penetrate nearer and nearer to the ovary, undoubtedly shows the presence of stimulants of great specificity akin to the "Individualstoffe" of Jost. We are wholly ignorant of the nature of these stimulants, but I am inclined towards a hypothesis differing somewhat from his. Experiments by several botanists, which I have been able partially to corroborate, point to a single sugar, probably of the hexose group, as the direct stimulant. The specific "Individualstoffe" I believe to reside in the pollen grains and to be in the nature of enzymes of slightly different character, all of which, except the one produced by the plant itself for the use of its own pollen or by other plants of identical germinal constitutions, can call forth secretion of the sugar that gives the direct stimulus. At least this idea links together logically the fact of the single direct stimulus and the need of "Individualstoffe" to account for the results of the crossing and selfing experiments. But whether or not this be the correct physiological inference, the crossing and selfing experiments call for a hypothesis that will account for no stimulation being offered the tubes from the plant's own pollen, while at the same time great stimulation is given the tubes from the pollen of nearly every other plant.

This is a straight mathematical problem, and it is hardly necessary to say that it is insoluble by a strict Mendelian notation such as Correns sought to give. This is obvious to any one familiar with the basic mathematics of Mendelism. On the other hand, a near Mendelian interpretation satisfies every fact.

Let us assume that different hereditary complexes stim-

ulate pollen tube growth and in all likelihood promote fertilization, and that like hereditary complexes are without such effect. One may then imagine any degree of heterozygosis in a mother plant and therefore any degree of dissimilarity between the gametes it produces, without there being the possibility of a single gamete having anything in its constitution not possessed by the somatic tissues of the mother plant. From the chromosome standpoint of heredity the cells of the mother plant are duplex in their organization; they contain N pairs. The cells of the gametes contain N chromosomes, one coming from each pair of the mother cell; but they are all parts of the mother cell and contain nothing that that cell did not contain. These gametic cells can not reach the ovaries of flowers on the same plant because they can not provoke the secretion of the direct stimulant from the somatic cells of that plant.

All gametes having in their hereditary constitution something different from that of the cells of a mother plant, however, can provoke the proper secretion to stimulate pollen tube growth, reach the ovary before the flower wilts and produce seeds. Such differences would be very numerous in a self-sterile species where cross-fertilization must take place; nevertheless like hereditary complexes in different plants should be found, and this should account for the small percentage of cross-sterility actually obtained. It must be granted that this hypothesis satisfies the facts, but that is not all. It is admittedly a perfectly formal interpretation, but from a mathematical standpoint,—granting the generality of Mendelian inheritance,—it is the only hypothesis possible that can satisfy the facts.

Let us now look into a few of the ramifications of the subject. Examinations of the pistils that have been sectioned after cross-pollination show a considerable variation in the rate of growth of individual pollen tubes, though our curves of growth have been made by taking the average rate of elongation. Is this variation a result

of chance altogether or must we assume a differential rate of growth increasing directly with the constitutional differences existing between the somatic cells and the various gametes? If we assume that any constitutional difference between the two calls forth the secretion of the direct stimulus to growth, chance fertilization by gametes of every type different from that of the mother plant will ensue; if there is a differential rate, selective fertilization will occur. This question can not be decided definitely at present, but two different lines of evidence point toward chance fertilization.

1. Flowers from a single plant pollinated by different males show no decided difference in rate of fertilization.

2. Color differences are transmitted in expected ratios.

Further, it will be recalled that beginning with the F_2 generation, sister plants crossed together have given us our F_3 and F_4 populations, and that these F_3 and F_4 populations apparently have given a constantly increasing percentage of cross-sterility. This is what should be expected under the theory that a small difference in germ plasm constitution is as active as a great difference in causing the active stimulation to pollen tube growth. Breeding sister plants together in succeeding generations causes an automatic increase of homozygosity as is well known. This being a fact, cross-sterility should increase. Such an increase in cross-sterility has been observed in the F_3 and the F_4 generations, but it would not be wise to maintain dogmatically that it is significant.

There are various questions, including the important one of the origin of self-sterility, that can not be discussed at this time. In conclusion, therefore, let us turn once more to the phenomenon of self-sterility in *Ciona intestinalis*. It seems to me that the hypothesis outlined above has few, if any, drawbacks when applied to self-sterility in plants. The question there, as far as we have gone, is one of pollen tube growth, and the theory that the secretion of the direct stimulant can be called forth only by a gamete that differs in its constitution from the somatic

cells between which the pollen tube passes, is logical. If the same theory is to be extended to animals, however, it follows that the external portions of the membranes of the animal egg that have been shown by the wonderful investigations of Loeb and of Lillie to have such important functions, must be functionally zygotic in character. I am aware that this suggestion may be considered pretty radical, but it certainly should be given consideration. I do not like to draw an analogy between the animal egg and a pollen grain, but it may be mentioned that in these structures—surely comparable to the animal egg in the fineness of their membranes and walls—both color and shape are inherited as if they were zygotic in nature.

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